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Larval and Early Postlarval Development of *Macoma mitchelli* Dall (Bivalvia: Tellinidae)

by

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Abstract. Specimens of *Macoma mitchelli* were spawned and the larvae and juveniles reared (ca.9‰ and 23°C) for 67 days. Recently spawned eggs measured 59 ± 2.3 μm. Straight-hinge larvae 70–80 μm long developed within 20 h of spawning, and pediveliger larvae settled into sand by day 6 or day 7 after spawning (approximate size range at settlement: 160–205 μm). A short exhalant siphon developed by day 15 (juvenile size range: 240–340 μm), but an inhalant siphon did not appear until some time between day 41 and day 52 (size range: 390–910 μm). Shell-hinge structure included a series of small denticles during larval developmental stages, development of an umbo at a shell length of 120–150 μm, appearance of a prominent ligament pit at a shell length of approximately 170 μm, and development of articulating cardinal teeth in animals larger than about 210 μm.

INTRODUCTION

Macoma mitchelli Dall, 1895 (=*Macoma phenax* Dall, 1900) is a burrowing tellinid bivalve found in meso-polyhaline waters of Chesapeake Bay, where it attains a maximum size of about 16 mm (BLUNDON & KENNEDY, 1982b; HINES & COMTOIS, 1985). The species has not been much studied, and most reports consist of a listing of its presence in samples collected during regional surveys of benthic biota along the Atlantic and Gulf Coasts of the United States (*e.g.*, PARKER, 1959; TENORE, 1972; REDDING & CORY, 1975). In Chesapeake Bay, *M. mitchelli* may be abundant in soft sediments (PFITZENMEYER & DROBECK, 1963; HINES & COMTOIS, 1985), with fluctuations in abundance apparently linked to seasonal predation (HOLLAND *et al.*, 1980; BLUNDON & KENNEDY, 1982a, b). Newly settled spat and small juveniles (<5 mm) have been found in benthic samples throughout the year (SHAW, 1965; BLUNDON & KENNEDY, 1982b).

We report here the results of laboratory spawning and rearing of *Macoma mitchelli*, including information on larval hinge structures. Such information should be useful to those seeking to identify larvae and juveniles in planktonic or benthic samples (LUTZ *et al.*, 1982).

MATERIALS AND METHODS

Adult bivalves were collected in the summer (ca.9‰ and 23°C) from the Choptank River, Maryland, offshore from Horn Point Environmental Laboratories (38°36'N;

76°09'W), and were held in bowls in running, cooled (18°C) river water. A number of attempts were made to spawn these adults by placing groups in clean bowls containing 1-μm-filtered river water (ca.9‰) and held in a water bath in which temperatures were varied periodically from about 18°C to 25°C. Water samples were collected and examined microscopically both before and after spawning occurred. After spawning occurred and we judged that a quantity of sperm had been released that was sufficient to fertilize the eggs present, the water in the bowls was washed through an 88-μm screen to remove debris and into a 30-L plastic garbage can containing 1-μm-filtered river water (ca. 9‰). Larvae were cultured at about 23°C in this container until they were ready to metamorphose.

Algal food (Tahitian *Isochrysis* sp. and *Chlorella* sp.) was provided daily (1:30 mix). The culture water was renewed every second day by retaining the larvae on screens, discarding the old culture water, and adding new 1-μm-filtered river water. A few milliliters of water from the larval culture were sampled daily, and larvae were examined microscopically until metamorphosis occurred. For 24 to 30 larvae, we measured shell length (maximum anteroposterior distance, μm) and height (maximum dorsoventral distance, μm) to the nearest 5 μm under a microscope with a calibrated ocular micrometer. When the larvae became pediveligers, they were placed in 1.5-L glass bowls, with sand on the bottom. After they had metamorphosed, juveniles continued to be held in bowls of sand, and measurements of length × height were continued irregularly for about two months; the juveniles were fed algae and examined until many were ca. 4 mm long. In addition to measuring the size of 10–25 juveniles each observation day, we made notes on their behavior and on changes in siphonal anatomy.

Samples of larvae and juveniles were preserved in 70% ethanol to provide material for photomicrographs of external shell morphology. Material for scanning electron microscopy was placed in distilled water for about 30 min and then preserved in 95% ethanol (Lutz *et al.,* 1982). Thereafter, specimens were taken from the preservative, rinsed in distilled water, and placed in a 5% solution of sodium hypochlorite for about 10 min. The resulting separated shell valves were rinsed in distilled water, mounted on silver tape, coated with ca. 600 Å of gold-palladium, and examined under an ETEC Autoscan scanning electron microscope. During scanning electron microscopic documentation of internal views of left and right valves, consistency of shell orientation was maintained by maneuvering each specimen so that four points (each 90° apart) along the shell edge were in the same plane of focus at about 30,000× (Lutz *et al.,* 1982). Shell dimensions were determined by comparison with standard grids photographed at the same magnification as each shell specimen.

RESULTS

Two attempts at spawning these clams were successful, with one producing few larvae and the other being more productive. Results from both attempts are consolidated for this report, but all shell measurements and photographs are those of animals from the more successful second spawning.

Adult males extended their exhalant siphon about three to four times the length of the clam during spawning, and muscular waves ran along the length of the siphon. Sperm were released in intermittent, smokelike puffs, although occasionally a steady stream of sperm was produced for a few seconds. The length of the head of a typical sperm was 5–10 μm, with a maximum width of 1–2 μm. Sperm tails were "pigtailed" in shape; their length was not determined.

Egg release was not observed, but eggs were found in water samples pipetted from the bowls within 90 min of stimulating clams by varying the temperature. Average egg size at this time was 59 ± 2.3 μm ($n = 25$). Eggs that had been in the presence of sperm for some time were seen to be surrounded by a sperm "aura," with the sperm apparently trapped in clear material (fertilization membrane?) about one-half the diameter of the egg away from its surface.

Straight-hinge larvae developed within 20 h after spawning, when larvae were 70–80 μm long (*e.g.,* Figure 1F). An apical flagellum was present and was retained until metamorphosis. A slight saddle shape in the hinge region, somewhat similar to the shell of the larger *Lyonsia hyalina* (Chanley & Castagna, 1966), was noted in 48-h larvae (80–85 μm). The "D shape" began to be lost by 94 h after spawning (95–115 μm), with a more oval shape becoming apparent (Figures 1B, 2). The umbo had become more prominent by 118 h (120–150 μm), and larval shape was more circular than oval. The anterior end of the shell was more prominent by 144 h (130–165 μm) and continued to develop as shown in Figures 1C–F, 3. As development continued, the broadly rounded umbo gradually became knobby (Figure 3) (Chanley & Andrews, 1971). A club-shaped foot was apparent in many larvae by 144 h, but it was used actively by only a few larvae >160 μm, whereas by 168 h (155–190 μm) the foot was active in many larvae. By day 6 (first batch of larvae) or day 7 (second batch), young clams responded to the presence of sand by digging. By this time most had lost their velum. Eyespots were not noted at any time during development. The approximate size range at metamorphosis was 160 μm (the size of the smallest larva noted to have an active foot) to 205 μm (the largest larva with an active foot and a functioning velum).

Metamorphosed animals (spat) tended to have particles adhering to the shell and were sometimes found to stick together (see also Webb, 1986). Larger animals had reddish shells (see also Chanley, 1969). By day 15 (240–340 μm), many juveniles had a short exhalant siphon that could be protruded from the shell and from which particles were occasionally expelled. Particles were also expelled from the opening of the shell below the siphon. No inhalant siphon was present, and particles were drawn into the mantle cavity at the end opposite the siphon end. Juveniles were examined on day 25 (300–400 μm), day 33 (350–

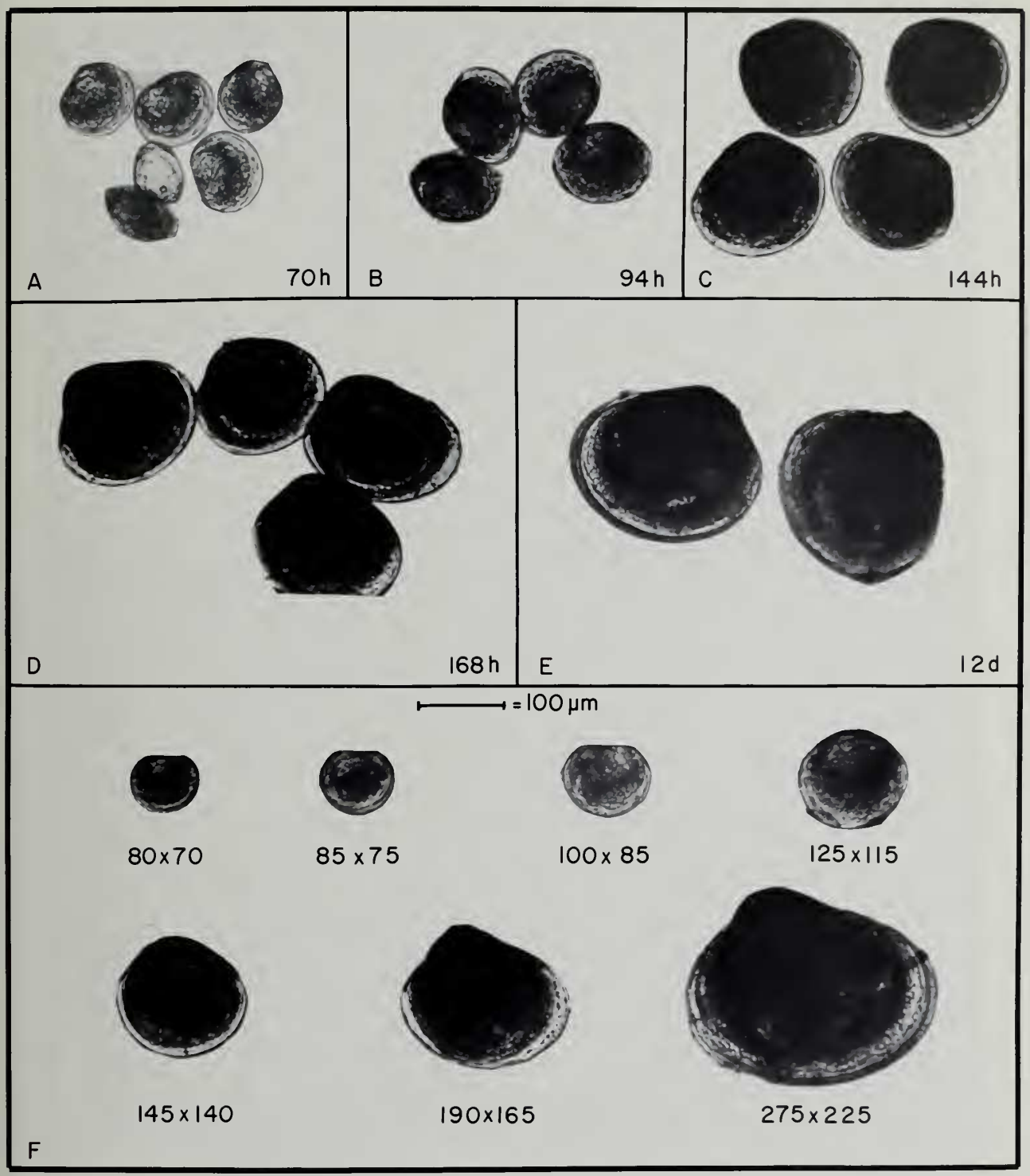

Figure 1

Photomicrographs of *Macoma mitchelli* larvae and postlarvae. A–E. Grouped clams ranging from 70 hours (h) to 12 days (d) old. F. Individual clams of representative lengths, with anterior end to right. Measurements (µm) are length × height. Scale line applies to all animals, including grouped clams.

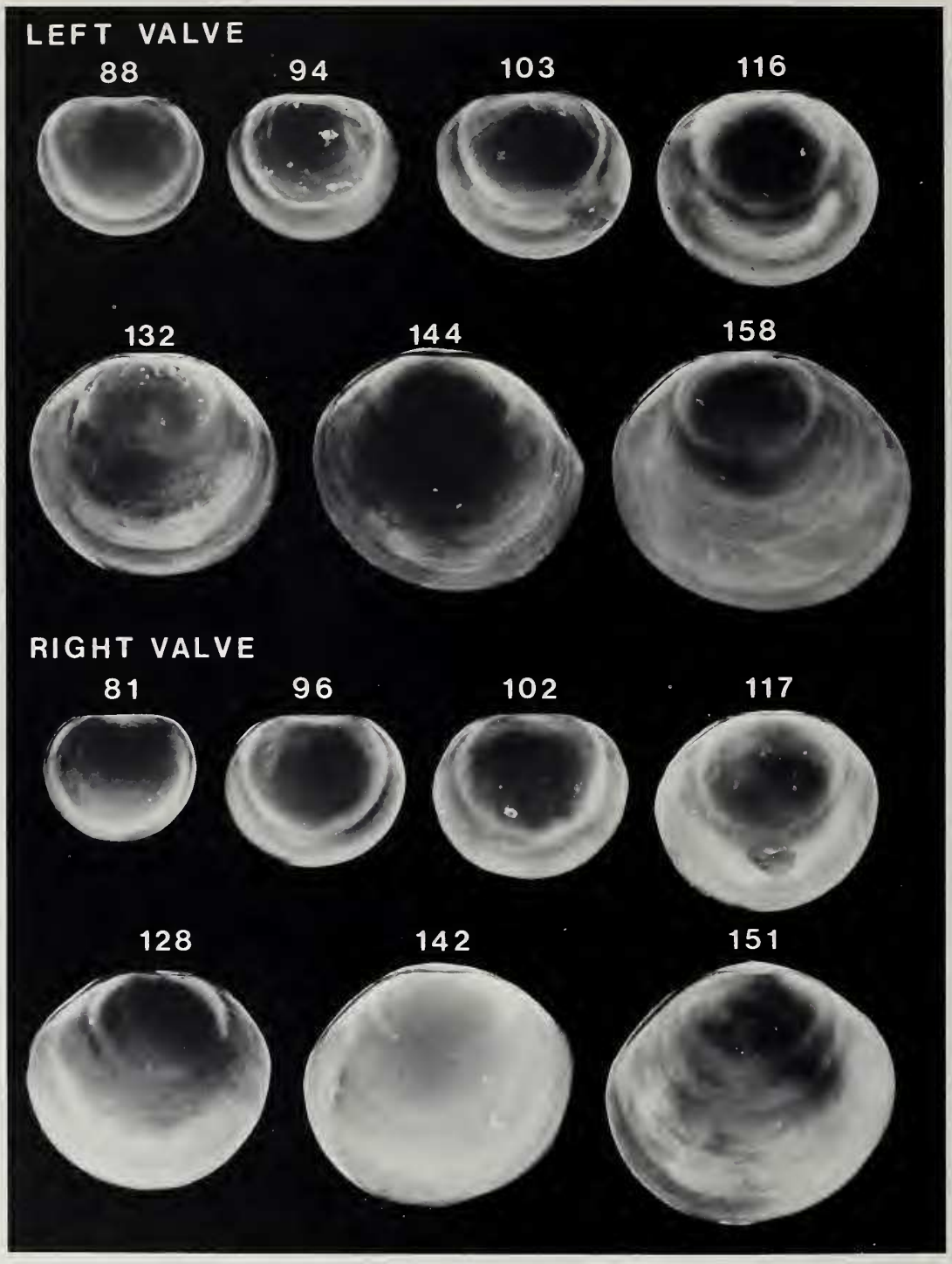

Figure 2

Scanning electron micrographs of interiors of disarticulated shell valves of *Macoma mitchelli* larvae. Numbers are shell length (μm).

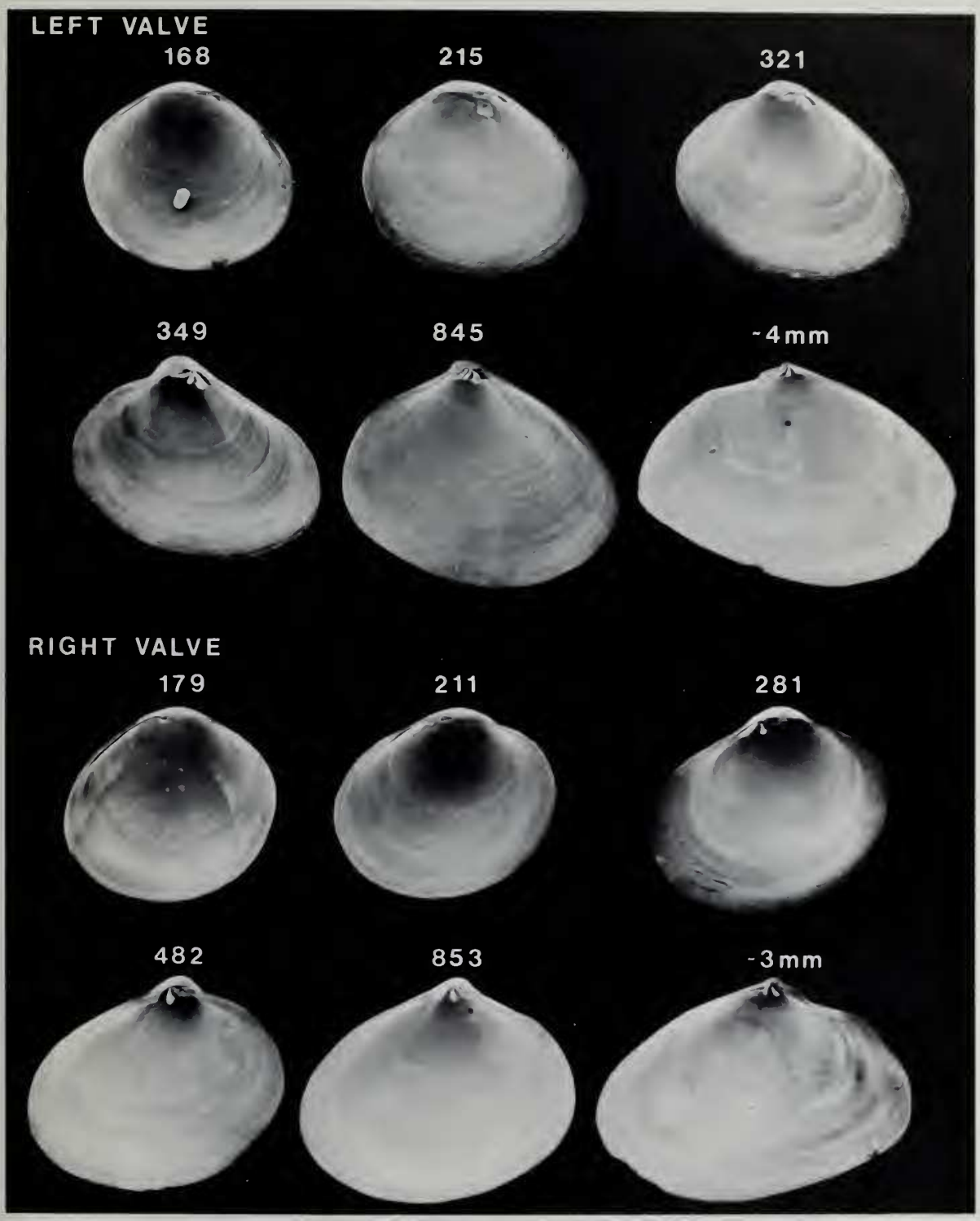

Figure 3

Scanning electron micrographs of interiors of disarticulated shell valves of *Macoma mitchelli* postlarvae. Numbers are shell length (μm).

Figure 4

Scanning electron micrograph of the exterior surface of an early postlarval valve (length, ca. 275 μm) of *Macoma mitchelli*. Arrow marks transition from commarginal to cancellate sculpture.

Figure 5

Scanning electron micrograph of the exterior surface of a shell of a 41-day-old *Macoma mitchelli* (length, ca. 600 μm).

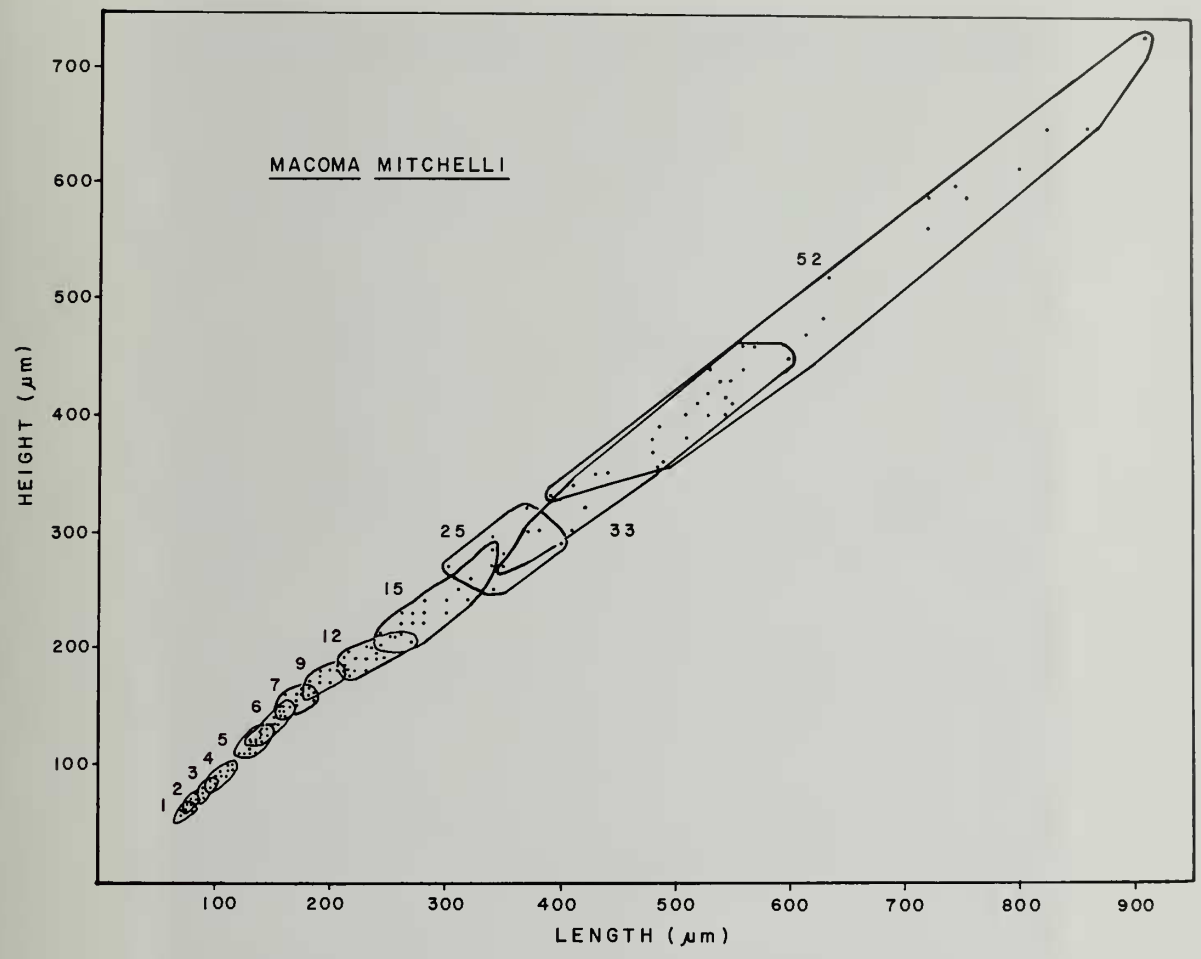

Figure 6

Length-height relationships (days 1–52) for *Macoma mitchelli* larvae and juveniles, to show increased size scatter over time. Metamorphosis occurred by day 7. Points may represent measurements on more than one animal.

600 μm), and day 41 (370–620 μm), but no inhalant siphon was noticed until day 52 (390–910 μm). All but the smallest clams had paired siphons by day 67. However, at no time was the inhalant siphon seen in use. Particles continued to enter the shell cavity ventrally, even in spat as large as 3.4 mm (day 67).

Examination of exterior shell morphology of early postlarval specimens showed an abrupt transition from commarginal to cancellate sculpture (Figure 4) at an average length of 193.8 ± 5.7 μm (range: 183–201 μm; n = 15). The postlarval shells were found to have distinct external commarginal ridges (*e.g.*, Figure 5; see also WEBB, 1986) when observed by light microscope on day 41 (shell length: 370–620 μm; ridge numbers: 4–11). Over 40 ridges were visible in the shells of clams >3.4 mm long (day 67). By day 67, most spat had attained the typical adult shape of *Macoma mitchelli* and possessed a wedge-shaped foot.

Separate linear regressions were fitted to data on length-height relationships for days 1–7 ($y = 1.6 + 0.90x$; $r^2 = 0.90$; $n = 159$, where y = height and x = length) and days 9–67 ($y = 23.2 + 0.74x$; $r^2 = 0.99$; $n = 120$) because there appeared to be a break in the curves between days 7 and 9 (Figure 6). This period of time encompassed the end of pelagic development and the beginning of benthic existence. Figure 6 also demonstrates increasing disparities in size among clams of the same age as time passed. By day 67, some animals were longer than 4.2 mm, while others were as small as 580 μm long.

Examination of larval and postlarval shell-hinge structures of the specimens shown in Figures 7 and 8 revealed numerous, small denticles on the larval hinge. A prominent ligament pit appeared at a shell length of approximately 170 μm; subsequent development of cardinal teeth on the anterior region of the postlarval hinge began when shells were approximately 210 μm long (Figure 8). After metamorphosis, the ligament pit of juveniles enlarged, as did

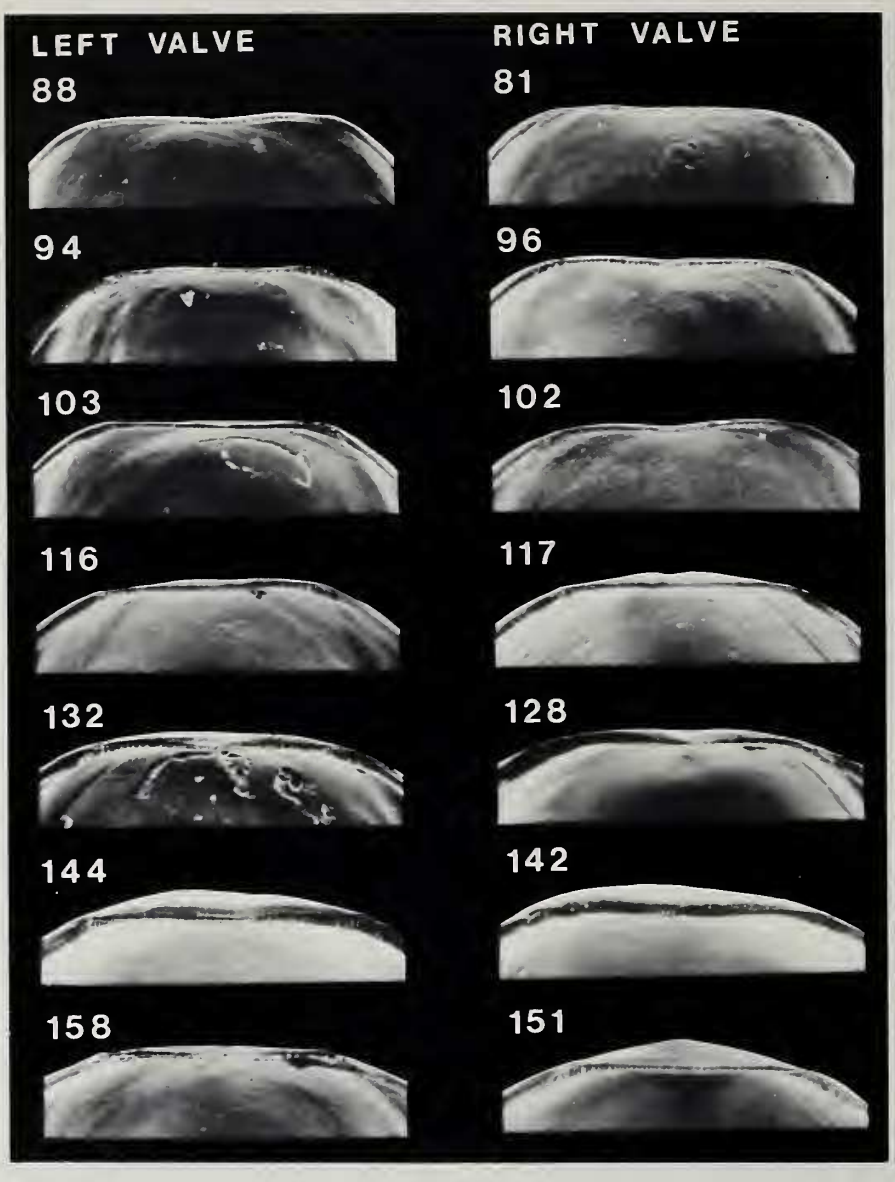

Figure 7

Scanning electron micrographs of the hinge apparatus of larval valves pictured in Figure 2. Numbers are shell length (μm).

the cardinal teeth on each valve (Figure 8). The articulating nature of these cardinal teeth is shown clearly in a comparison of left and right hinge structures of the larger animals pictured (Figure 8). At a shell length of approximately 3 to 4 mm, cardinal teeth had differentiated into laminate and bifid forms (Figure 8).

DISCUSSION

Although our objective was to rear and describe larval and postlarval stages of *Macoma mitchelli*, some of our observations have relevance to results of other studies. *Macoma mitchelli* developed and metamorphosed quickly compared with other species studied on the east coast of North America, most of which are reported to require 10 or more days to reach metamorphosis (Loosanoff & Davis, 1963; Chanley & Andrews, 1971). However, a few east coast species are known to develop about as quickly as *M. mitchelli*. At 20°C, *Laevicardium mortoni* metamorphosed by eight days after fertilization (Loosanoff & Davis, 1963). *Rangia cuneata* (an oligohaline species found in Chesapeake Bay) began to set at a size range of 160–175 μm after seven days at 22–24.4°C (Chanley, 1965). *Lyonsia hyalina* (Chanley & Castagna, 1966) began meta-

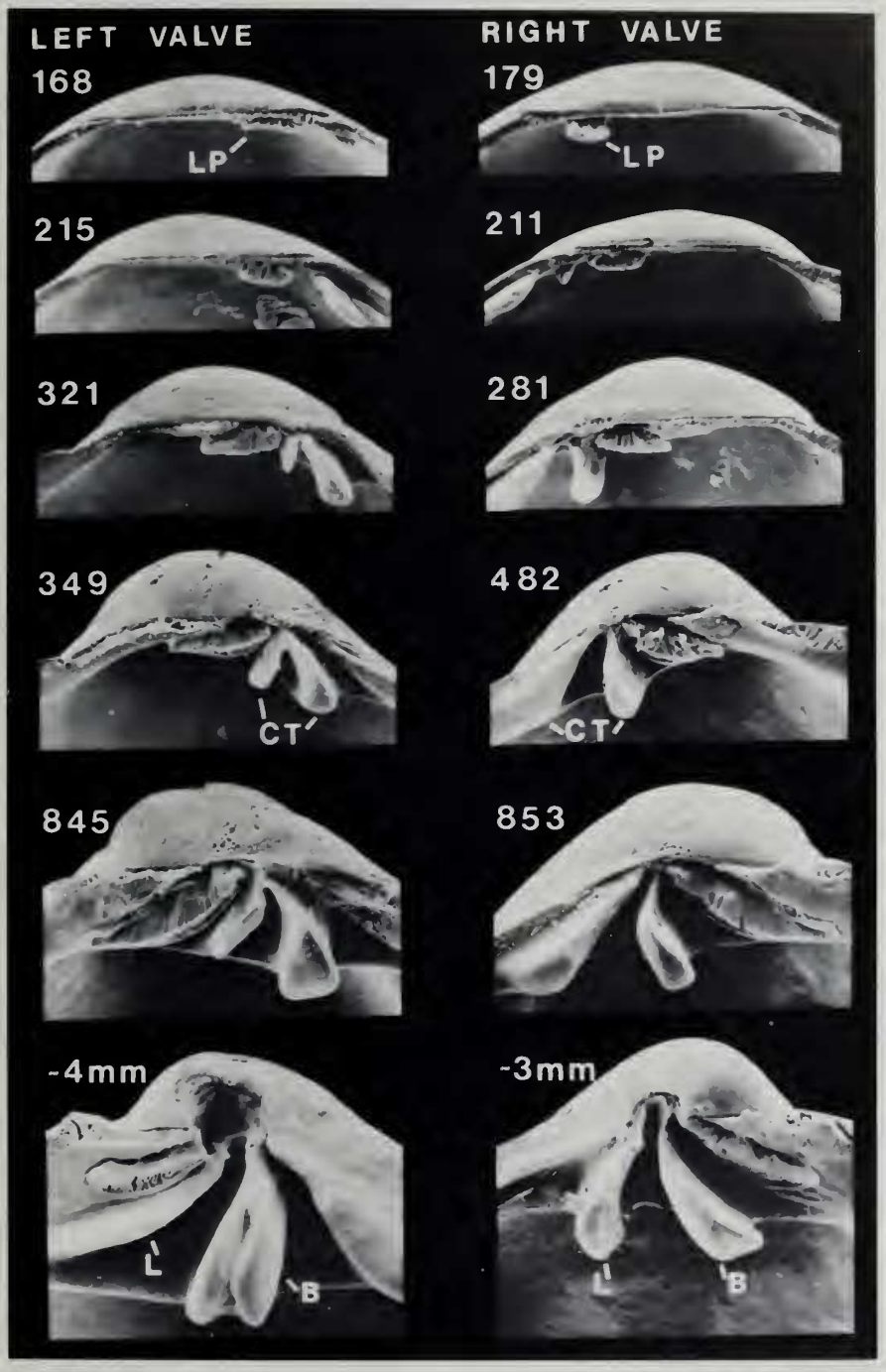

Figure 8

Scanning electron micrographs of the hinge apparatus of postlarval valves pictured in Figure 3. Numbers are shell length (μm). CT, cardinal teeth; LP, ligament pit; B, bifid cardinal tooth; L, laminate cardinal tooth.

morphosis three days (18–22°C) after fertilization at sizes ranging from 155 to 175 μm (see also CAMPOS & RAMORINO [1981] for data on rapid settlement of the lyonsiid *Entodesma cuneata* in Chile). *Macoma balthica* in Chesapeake Bay can also settle in less than one week at about 21°C (personal observations).

During development, the external morphology of *Macoma mitchelli* (pronounced anterior end, knobby umbo,

commarginal ridges) resembled that of other tellinids (*e.g.*, CHANLEY & ANDREWS, 1971; WEBB, 1986). However, the external morphology of juvenile *M. mitchelli* does not resemble that of juvenile *M. balthica,* the other common tellinid in central and upper Chesapeake Bay, in that the latter retains the more circular outline of the adults (personal observations). Internally, the ligament pit in *M. mitchelli* (Figure 8) did not appear to develop until larvae had reached the size range for metamorphosis, supporting the suggestion by LUTZ & HIDU (1979) that such structures are postlarval features. Similarly, as postulated for tellinacean larvae by CHANLEY (1969) and shown for postlarval *Tellina fabula* by WEBB (1986), development of the cardinal teeth was most noticeable after metamorphosis (Figure 8; postlarvae >210 μm). While a ligament pit formed early in metamorphosis (visible in specimens with a shell length as small as 168 μm [Figure 8]), dissoconch cancellate sculpture was not apparent until a size of 183–201 μm.

Limited information is available on morphological development of soft-body parts of young bivalves, such as development of the siphon. The exhalant siphon seemed to develop more slowly in *Macoma mitchelli* than in the tellinid *Abra alba* (AABEL, 1983) in which the siphon can extend beyond the shell margin at metamorphosis. Such behavior was not noted in *M. mitchelli* until day 15 after spawning. As in *A. alba,* newly settled *M. mitchelli* had no inhalant siphon. The inhalant siphon develops in *A. alba* at the end of the third month after settlement (at 10°C), at a shell length of about 1 mm (AABEL, 1983). In *M. mitchelli,* an inhalant siphon was not noticed on day 41 but was apparent in some clams at day 52 (animals <1 mm), with most clams possessing paired protrusible siphons on day 67. As in juvenile *A. alba,* in the absence of a functioning inhalant siphon, currents established by individual *M. mitchelli* brought suspended particles in through the ventral opening of the shell. Because no inhalant siphon was observed to be in use during our observations of juvenile *M. mitchelli,* we cannot provide information to compare with the changed method of particle uptake found in *A. alba* after the inhalant siphon comes into use. However, we suspect that feeding behavior would be similar in *M. mitchelli.*

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